Field Resistance of Two Soybean Germplasm Lines, HC95–15MB and HC95–24MB, Against Bean Leaf Beetle (Coleoptera: Chrysomelidae), Western Corn Rootworm (Coleoptera: Chrysomelidae), and Japanese Beetles (Coleoptera: Scarabaidae)

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ABSTRACT   Two recently released, Mexican bean beetle, *Epilachna varivestis*, Mulsant, resistant soybean, *Glycine max* (L.) Merrill, germplasm lines, HC95–15MB and HC95–24MB, were examined for foliar and pod feeding resistance to adult bean leaf beetles, *Cerotoma trifurcata* (Förster), western corn rootworms, *Diabrotica virgifera virgifera* LeConte, and Japanese beetles, *Popillia japonica* Newman. Both lines were planted along with a susceptible control cultivar in 18 by 30-m plots and separate 0.8-ha size fields. Insects were sampled on a weekly basis with a sweep net. In late summer, defoliation ratings were recorded along with data on percentage pod feeding. Although a few significant differences in insect densities were obtained among the soybean lines on some sampling dates, no specific trends were observed in the ability of the resistant germplasm to reduce insect numbers. Insect population densities were similarly on all lines. However, both resistant lines were able to reduce defoliation during the growing season. Conversely, percentage pod feeding was similar among all the soybean lines, with no differences observed. The resistant germplasm lines appear able to lower levels of defoliation, and thus, offer a potential management tactic where leaf feeding, i.e., defoliation, is of concern. However, their ability to greatly reduce beetle population densities, and for the bean leaf beetle, to reduce pod feeding, appears limited.

KEY WORDS   *Cerotoma trifurcata*, *Diabrotica virgifera virgifera*, *Popillia japonica*, soybeans, host plant resistance,

ALTHOUGH A FEW soybean, *Glycine max,* (L.) Merrill, cultivars with insect resistance have been developed and released in the United States, none have been widely accepted by growers because of a lack of high yields and sufficient insect control (Boethel 1999). However, breeders and entomologists have made gains in developing and releasing soybean germplasm lines that are used in breeding programs. Although germplasm lines do not have yields equal to commercial varieties, they do offer breeding material with moderate yields and levels of insect resistance for crossing purposes.

Recently, two insect-resistant lines, HC95–24MB and HC95–15MB, having much higher yields while maintaining moderate to high levels of resistance compared with previously released germplasm lines, were released (Cooper and Hammond 1999, Hammond and Cooper 1999). These lines were developed using the laboratory antibiosis screening technique (LAST) procedures (Rufener et al. 1987) where selection was based on the relative mortality and development of Mexican bean beetle, *Epilachna varivestis* Mulsant, larvae. HC95–24MB and HC95–15MB are selections from the cross 'Hobbit 87' × HC83-123-9, with the latter parent being an insect resistant germplasm line from the cross 'Pixie' × PI229358. This latter source is one of the first defoliation resistant lines identified in the late 1960s (Van Duyn et al. 1971, 1972).

Over the past 5–10 yr, Ohio, as well as much of the Midwest has been experiencing increasing problems with the bean leaf beetle, *Cerotoma trifurcata* (Förster). The bean leaf beetle defoliates soybeans throughout most of the summer during its adult stage, feeding on pods in the later part of the growing season. Pod feeding not only results in direct yield loss, but allows for the entrance of secondary seed pathogens which can result in a loss of seed quality (Pedigo 1994). Compared with the Mexican bean beetle, in which both larvae and adults feed on soybean leaves, the bean leaf beetle oviposits in the soil, and then larval development and feeding occurs on the roots and nodules. Although the original source of resistance, PI229358, has been shown to exhibit some foliar resistance against the bean leaf beetle adults (Clark et al. 1972, Layton et al. 1987), HC95–15MB and HC95–

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24MB have not been tested against this insect in the field.

Another insect situation associated with soybean has occurred with potential serious ramifications for growers. Western corn rootworms, *Diabrotica virgifera virgifera* LeConte, normally oviposit in corn, *Zea mays* L., fields causing significant root-feeding injury the following year when again planted to corn. Thus, continuous corn is most likely to have western corn rootworm problems, whereas noncrop rotation will avert the problem. Recently, a new strain of the western corn rootworm has developed that feeds on soybean leaves and oviposits in soybean fields as an adult in the eastern portions of the corn belt (Levine and Oloumi-Sadeghi 1996, Onstad et al. 1999, Spencer et al. 1999,). Although economic injury to soybean from defoliation is unlikely, the western corn rootworm larvae that hatch the following year can cause root injury to corn. Thus, the practice of crop rotation with soybean to manage the western corn rootworm problem diminished in certain areas. Because of this phenomenon, growers are interested in the potential for soybean resistant to feeding by western corn rootworm.

We conducted fields studies in Ohio and Illinois to determine the relative resistance of HC95–15MB and HC95–24MB to bean leaf beetle, western corn rootworm, and Japanese beetle, *Popillia japonica* Newman. The Japanese beetle is another soybean pest capable of causing moderate levels of defoliation on soybean that occurred in the Ohio plots. Our objectives were to determine whether these resistant soybean germplasm lines offer potential resistance to these beetles by reducing insect population densities, lowering levels of defoliation, and reducing pod injury in the field.

Materials and Methods

Ohio. Insect-resistant soybean germplasm lines, HC95–24MB and HC95–15MB, were planted in southern Ohio near Piketon, OH. A commercially available variety, cultivar 'Troll', was also planted. No commercially grown lines, including Troll, are considered to have any levels of insect resistance. Plots were ≈18 by 30 m, with four replications. The lines are determinate semidwarf lines that are shorter than the typical indeterminate cultivars commonly grown in the Midwest. HC95–15MB and Troll are Group Maturity IV, whereas HC95–24MB is a late Group Maturity III. Soybeans were planted in narrow rows (20 cm wide) using a planting drill. Planting dates were 6 May 1999 and 9 May 2000. Preemergent herbicides, common to the area, were applied within 48 h of planting. Soil type was Huntington silt loam.

After emergence, plants were observed for the presence of overwintered bean leaf beetle and defoliation. Insects were sampled every week from growth stage V4 (Fehr and Caviness 1977) until plants began to mature. Two 25-sweep samples were taken in each plot, bagged, and returned to the laboratory where insects were counted and recorded. During the summer, defoliation levels were observed. In late July,

estimates of percentage defoliation were taken at five locations throughout the plot by two people selected without having knowledge of what treatments were in which plot. Data on pod injury were recorded beginning at growth stage R5. The total number of injured and noninjured pods was recorded from 10 randomly selected plants. These data were collected twice in early September. Although the lines grown are from different maturity groups, all three were observed to be in the same growth stage on all sampling dates (data not included).

In the second year, the three lines were also planted in ≈0.8 ha fields. This was done to determine if results obtained in the replicated plots would be observed in field-size areas. These fields, planted on 9 May, measured 91 by 91 m. However, because of their larger size and lack of additional land, these fields were not replicated. Fields were sampled weekly for insects as in the plots; however, 10 net samples (25 sweeps) were taken in each field. Similar data on pod injury were collected by randomly selecting 30 plants per field; observations on defoliation were also recorded throughout the summer.

Illinois. Similar procedures were used in Illinois in 1999. Soybean planting date was 28 May 1999. Plot size was 12.2 by 21.3 m with four replications, and row width was 76.2 cm. An additional commercially available soybean line, cultivar 'Macon', was included in the experiment. Macon is an indeterminate, late Group Maturity III line, reaching a taller height than the other three lines. Soil type was Plano silt loam.

Weekly sweep-net sampling began on 2 July and terminated on 2 September. Sweep-net samples consisted of 20 sweeps per sample compared with 25 sweeps per sample in Ohio, and only one sample was taken per plot. Pod injury data were collected on 2 September, by recording percentage injury from 10 plants per plot. Defoliation estimates were also taken on that date.

Data Analyses. Insect data for bean leaf beetle and western corn rootworm adults were transformed before analyses with square root $(x + 0.5)$, and for Japanese beetle log $(x + 0.5)$ to stabilize the variance. The former was used because of the random distribution that bean leaf beetle and western corn rootworm are known to have, and the latter used because Japanese beetles are known to have a contagious distribution pattern. Percentage pod injury data were transformed before analyses by arcsine (square root [X]). Data from the replicated plots were analyzed using analysis of variance (ANOVA) procedures in SAS (SAS Institute 1988) and means separated using least significant difference (LSD) at the 5% level. Data from the large fields in Ohio in the second year could not be analyzed using ANOVA procedures because of a lack of replication. However, means and standard errors were calculated and the results graphed, and standard *t*-tests used to compared the insect population means from each soybean line.
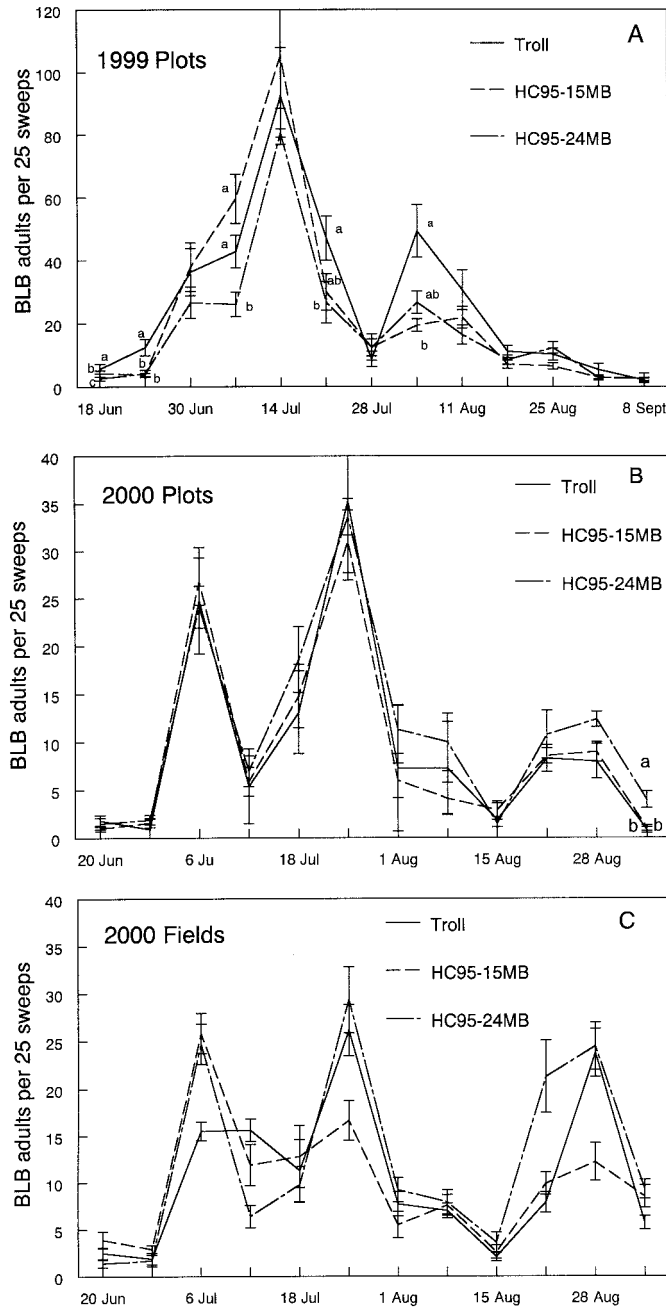
Fig. 1. Mean number (±SEM) of adult bean leaf beetles in Ohio in 1999 and 2000. Letters associated with sampling date indicate that a significant difference was obtained, with treatment means having the same letter not differing significant according to LSD ($P < 0.05$).

Results

Ohio. Population densities of bean leaf beetle were similar among the three soybean lines grown in the plots both years (Fig. 1A and B). There were a few sampling dates where statistical differences were obtained in 1999. In June, the highest bean leaf beetle density was on Troll, albeit < 5 adults per sample,

while the lowest numbers occurred on HC95–24MB (18 June: $F = 38.8$; df = 2, 6; $P < 0.01$, 23 June: $F = 5.4$; df = 2, 6; $P = 0.05$). On 7 July, densities were lowest on HC95–24MB ($F = 11.0$; df = 2, 6; $P = 0.01$), and on 21 July and 4 August, densities were slightly higher on Troll (21 July: $F = 5.5$; df = 2, 6; $P = 0.04$, 4 August: $F = 5.3$; df = 2, 6; $P = 0.05$). However, with the possible exception on the 4 August sample, the differences

Table 1. Statistical data for analyses for the field size plots in 2000

Soybean line comparison	df	t	P
		6 Jul	
Troll vs HC95-15M	9	3.8	<0.01
Troll vs HC95-24MB	9	3.7	<0.01
		23 Jul	
HC95-15MB vs Troll	9	2.4	<0.02
HC95-15MB vs HC95-24MB	9	3.0	<0.01
		28 Aug	
HC95-15MB vs Troll	9	3.8	<0.01
HC95-15MB vs HC95-24MB	9	6.6	<0.01
		22 Aug	
Troll vs HC95-24MB	9	3.1	<0.01
HC95-15MB vs HC95-24MB	9	3.3	<0.01

were not large. Bean leaf beetle populations reached high enough densities on all three lines to have caused growers concern. The densities on the 21 July and 4 August dates, when statistical differences were obtained, ranged from 25 to 40 adults per 25 sweeps on the lines. When bean leaf beetle populations peaked on 14 July, densities on the three lines were >80 adults per 25 sweeps. This level of adults, ≈3.2 per sweep, is considered near or over the economic threshold depending upon the value of the crop and cost of treatment (Pedigo 1994). The densities within the plots in 2000, while lower, were similar on most sampling dates with the exception of the last sampling date, 5 September ($F = 9.2$; df = 2, 6; $P = 0.02$), when HC95–24MB had more bean leaf beetle than did HC95–15MB or Troll. Population density reached a peak of >30 adults per 25 sweeps on 25 July

Confirming results were obtained in the larger fields in 2000 (Fig. 1C). Although variation was observed, bean leaf beetle densities were nevertheless similar among the lines, with the two resistant germplasm lines unable to reduce adult bean leaf beetle numbers compared with the susceptible line with only a few exceptions. On 6 July, densities were actually lowest on Troll, with t-tests indicating a significant difference compared with the two resistant lines (see Table 1 for statistical values). With the exception of HC95–15MB having a lower density on 23 July and 28 August, and both HC95–15MB and Troll having lower densities than HC95–24MB on 22 August (see Table 1), differences in adult densities in the larger fields (Fig. 1C) were similar to those in the plots (Fig. 1B).

Although some significant differences were obtained, populations of Japanese beetles in the plots were relatively low both years. Both resistant lines had fewer adults on 7 July 1999 in the plots (Fig. 2A) ($F = 6.7$; df = 2, 6; $P = 0.03$). During the second year (Fig. 2B), HC95–15MB usually had the fewest Japanese beetles, with significant differences obtained on 6 July and 1 August 2000 ($F = 6.9$; df = 2, 6; $P = 0.03$, $F = 18.8$; df = 2, 6; $P < 0.01$, respectively). Although some differences were observed with Japanese beetle densities in the larger fields, no trends were evident (Fig. 2C).

Western corn rootworm adults were collected in sufficient numbers to analyze only in 1999 on two dates. Adult numbers per 25 sweeps were 4.5 ± 1.1, 2.9 ± 1.0, and 3.3 ± 0.9 on 7 July, and 2.4 ± 1.2, 0.5 ± 0.3, and 1.3 ± 0.6 on 14 July for Troll, HC95–15MB, and HC95–24MB, respectively. Statistical differences were not obtained either date.

There were noticeable differences in the level of defoliation between the soybean lines grown in the plots throughout the summer in both years (R.B.H., unpublished data), with greater leaf feeding occurring in 1999 when population densities of bean leaf beetle were higher. Plots could easily be differentiated as early as mid-June based on the amount of feeding in the Troll plots compared with the two resistant germplasm plots, with the leaf feeding being from overwintered bean leaf beetle adults. Percentage defoliation in 1999 in late July, taken by two people following feeding by first generation adults, averaged 22.5%, 14.8%, and 10.0% for Troll, HC95–15MB and HC95–24MB, respectively. These levels were statistically different from each other ($F = 42.8$; df = 2, 6; $P < 0.01$). Generally, levels > 15–20% are considered above threshold if defoliation rates are used as a treatment criteria for many insects (Edwards et al. 1994, Hammond 1994, Sullivan and Boethel 1994). Defoliation was much lower in 2000, with defoliation levels of 3.9, 4.1, and 8.5% for HC95–15MB, HC95–24MB, and Troll, respectively. Although defoliation was low, these levels were statistically different ($F = 76.5$; df = 2, 6; $P < 0.01$). In the field areas in 2000, levels of defoliation were noticeably higher in the Troll field compared with the two resistant fields (R.B.H., unpublished data; no data recorded), comparable to differences observed in the soybean lines planted in the plots.

There were no significant differences in percentage pod injury obtained in the plots either year in Ohio (Table 2) (1 September 1999: $F = 0.48$; df = 2, 6; $P = 0.64$; 8 September 1999: $F = 0.36$; df = 2, 6; $P = 0.71$; 5 September 2000: $F = 0.04$; df = 2, 6; $P = 0.95$; 14 September 2000: $F = 0.6$; df = 2, 6; $P = 0.94$). On the two dates in 1999, percentage injury averaged around 25%, while in 2000, the average was much lower ranging from 2.0 to 5.5%. The lower percentage obtained in the second year was because of the lower bean leaf beetle populations (Fig. 1B). In the field in 2000, percentages of pod injury on 14 September were also comparable among the lines, Troll: 5.5% ± 1.2; HC95–15MB: 6.2% ± 1.4; HC95–24MB: 6.1% ± 1.2, which was similar to the injury on the three lines in the plots for that same date.

Illinois. Bean leaf beetle populations were relatively low throughout much of the summer in 1999 (Fig. 3A) compared with Ohio's densities. Densities in mid-July reached peaks of around 20 per 20 sweeps compared with Ohio's peaks at the same time of around 80 adults per 25 sweeps. Populations increased greatly in late August and early September when densities of second generation adults reached levels >100 adults per 20 sweeps. However, on these dates, significant differences were not obtained. The density of bean leaf
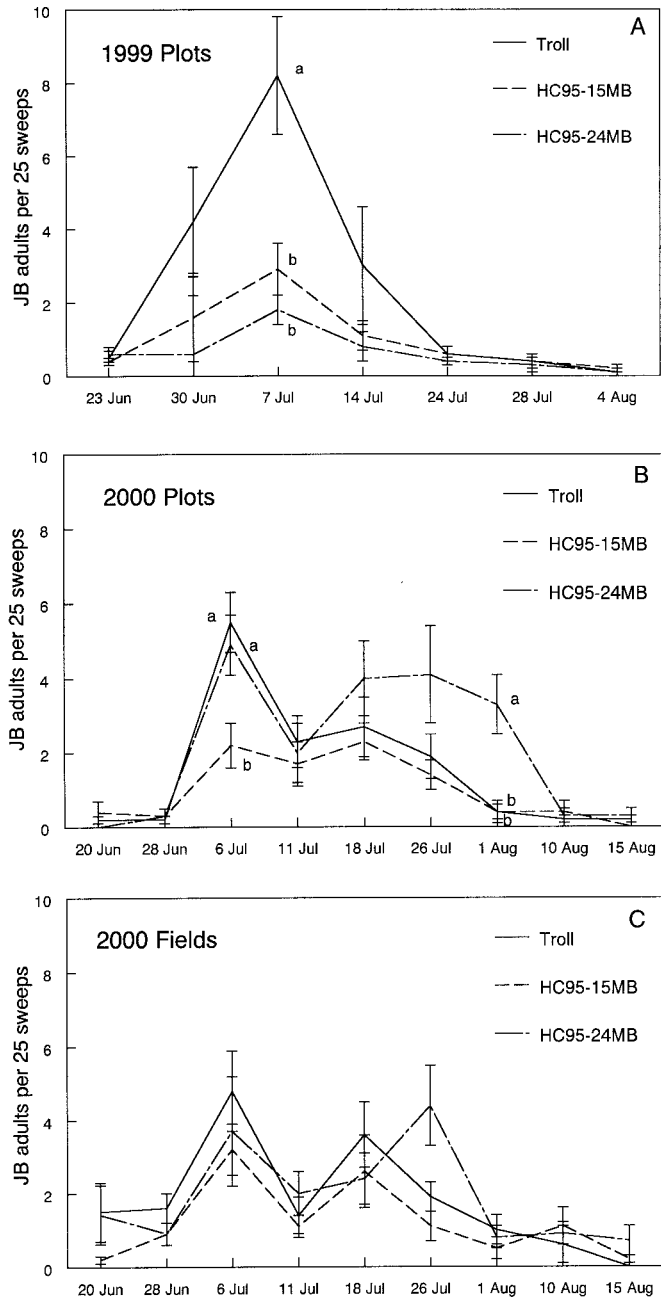
Fig. 2. Mean number (±SEM) of adult Japanese beetles in Ohio in 1999 and 2000. Letters associated with sampling date indicate that a significant difference was obtained, with treatment means having the same letter not differing significant according to LSD (P < 0.05).

beetle adults increased greatly on all four lines examined in Illinois, including the two resistant lines.

Significant differences were obtained in western corn rootworm densities (Fig. 3B) during part of the summer (2 August: F = 8.0; df = 3, 9; P = < 0.01, 9 August: F = 66.4; df = 3, 9; P = < 0.01, 23 August: F = 5.7; df = 3, 9; P = 0.02). Western corn rootworm adults were consistently higher on Macon compared with

the other lines. However, the population density on Troll, the other susceptible line in the study, was similar to those on the two resistant lines.

Percentage defoliation averaged 15.8, 11.3, 10.0, and 9.9% for Troll, Macon, HC95–15MB, and HC95–24MB, respectively. Troll was statistically higher than the other three lines (F = 5.8; df = 3, 9; P = 0.02). Macon had a greater percentage of pod injury than the two

Table 2. Percentage pod injury (±SEM) among soybean lines in Ohio and Illinois

Soybean line	Ohio				Illinois
	1 Sep 99	8 Sep 99	5 Sep 00	14 Sep 00	2 Sep 99
Troll	27.8a ± 3.5	21.4a ± 3.4	2.0a ± 0.6	5.2a ± 1.3	15.6ab ± 1.6
HC95-15MB	22.2a ± 3.6	27.6a ± 2.7	2.6a ± 0.8	5.7a ± 1.5	12.8b ± 1.1
HC95-24MB	26.3a ± 3.0	24.0a ± 3.2	2.1a ± 0.6	5.7a ± 1.2	10.7b ± 1.3
Macon[a]	—	—	—	—	22.4a ± 1.7

Numbers followed by different letters are significantly different at the 5% level by LSD.
[a] Macon was only tested in Illinois.

resistant lines ($F = 5.6$; df = 3, 9; $P = 0.02$) (Table 2), although pod injury on Troll was not different than percentages from HC95–15MB and HC95–24MB.

Discussion

The majority of insect-resistant breeding programs on soybean, especially those in the United States, have been directed toward foliar feeding lepidopteran pests. Efforts against insects that feed on both foliage and pods, e.g., the bean leaf beetle, have been relatively limited (Boethel 1999), with the corn earworm, *Helicoverpa zea* (Boddie), receiving the most atten-

tion. The majority of the effort toward this pest has been associated with its foliar feeding ability. Pod feeding resistance breeding programs have been mostly limited to injury caused by the stinkbug complex. Of note, there are efforts in Asia against two important pod feeding lepidoteran pests, the soybean pod borer, *Leguminivora glycinivorella* Matsumura (Guo and Feng 1984), and the limabean pod borer, *Etiella zinchenella* (Trictsche) (Talekar and Chen 1994).

Although the original sources of resistance identified in the late 1960s were tested for resistance to the bean leaf beetle, it was mostly for foliar feeding. Much
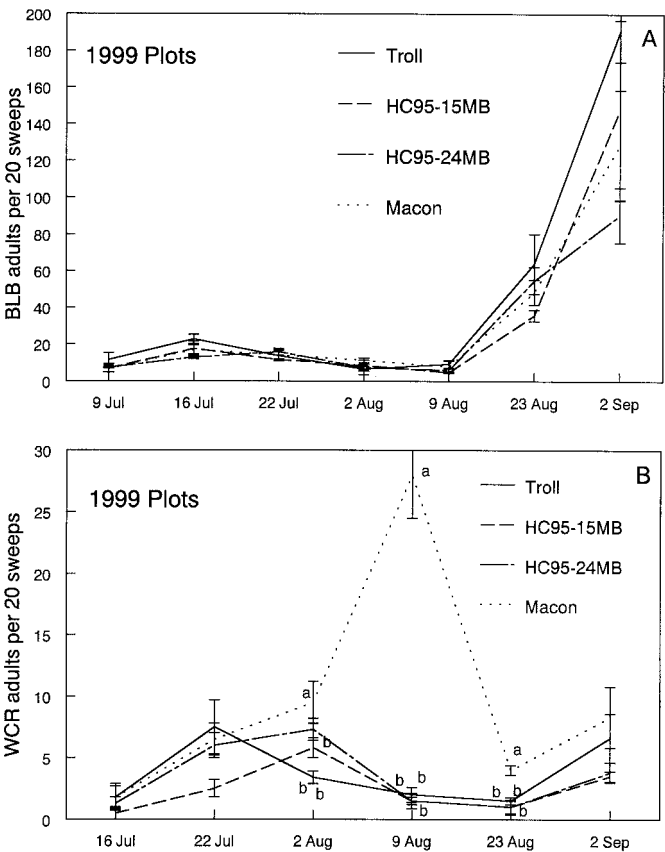

Fig. 3. Mean number (±SEM) of adult bean leaf beetles and western corn rootworms in Illinois in 1999. Letters associated with sampling date indicate that a significant difference was obtained, with treatment means having the same letter not differing significant according to LSD ($P < 0.05$).

of the newer germplasm that has been developed has not been examined for bean leaf beetle resistance under field situations, nor against the insect's ability to injure pods. Having examined these newer germplasm lines, HC95–15MB and HC95–24MB, in the field against bean leaf beetle, we found that they do offer resistance against bean leaf beetle foliar feeding, supporting earlier work (Clark et al. 1972, Layton et al. 1987). The ability to significantly reduce bean leaf beetle population density and subsequent pod feeding was low in our studies. Pod feeding resistance was not shown in plots nor in larger fields. The reason for this apparent a lack of resistance to pod feeding is unknown. However, studies have shown that levels of resistance decline with plant maturity (Nault et al. 1992a, 1992b; Hammond et al. 1995), and thus, any potential resistance in late season was negated.

Although the adult western corn rootworm normally does not cause foliar feeding injury significant enough to affect yield where the new strain occurs, there has been some concern that western corn rootworm may be able to transmit bean pod mottle virus which is known to be transmitted by bean leaf beetle (Hartman et al. 2001,m Spencer et al. 2001). Although the total impact of this virus is unknown, it has become more common in the Midwest the past few years (Spencer et al. 2001). The Illinois data suggest that defoliation levels, when caused partially by western corn rootworm, is lower in the resistant germplasm lines. However, significant reductions in population densities were not observed with this insect on the two resistant lines tested, similar to the lack of reductions observed with the bean leaf beetle. This was at least the case when the two resistant lines, HC95–15MB and HC95–24MB, were compared with their similar susceptible line, Troll (these three lines all being determinate semidwarf lines). However, adult western corn rootworm densities were higher on Macon, the additional susceptible line grown in Illinois, in early August. The reason for this is unclear, but the height differences between Macon compared with the other three lines (E.L., unpublished data) is a possibility. The lead author has seen similar differences among lines varying in height in previous germplasm comparisons (R.B.H., unpublished datas).

The inability of the lines to reduce population densities of these beetle species perhaps is related to how these lines were developed. The selection criteria in the LAST breeding program, from which these lines were selected, were slower larval development and higher larval mortality (antibiosis). Antixenosis is often observed with adult Mexican bean beetle, but neither adult mortality nor behavior was a selection criteria. Our observations indicate that while resistant soybean germplasm lines are able to cause significant mortality to insect larvae (Hammond and Cooper 1999), they do not cause significant mortality to adults. The reduction in foliar feeding in our study was apparent, and is most likely because of antixenosis compared with antibiosis. The ability to reduce feeding did not correspond to a reduction in population densities

of the beetles, nor to subsequent pod feeding by the bean leaf beetle.

These and other germplasm lines using PI229358 as a parent offer breeders a source of potential resistance against coleopteran foliar feeders in reducing the level of defoliation. The ability to prevent or reduce pod feeding from the bean leaf beetle appears limited. Their role in reducing western corn rootworm densities is questionable, although further work done over multiple years and locations, and under varying insect pressure, might prove otherwise.

References Cited

Boethel, D. 1999. Assessment of soybean germplasm for multiple insect resistance, pp. 101–129. *In* S. L. Clement and S. S. Quisenberry, [eds.], Global Plant Genetic Resources for Insect Resistant Crops. CRC, Boca Raton, FL.

Clark, W. J., F. A. Harris, F. G. Maxell, and E. E. Hartwig. 1972. Resistance of certain soybean cultivars to bean leaf beetles, striped blister beetles, and bollworm. J. Econ. Entomol. 65: 1669–1672.

Cooper, R. L. and R. B. Hammond. 1999. Registration of insect-resistant germplasm lines HC95–24MB and HC95–15MB. Crop Sci. 39: 599.

Edwards, C. R., D. A. Herbert, Jr., and J. W. Van Duyn. 1994. Mexican bean beetle, pp. 71–72. *In* Handbook of Soybean Insect Pests, L. G. Higley and D. J. Boethel, [eds.], Entomological Society of America, Lanham, MD.

Fehr, W. R. and C. E. Caviness. 1977. Stages of soybean development. SR80, Iowa State University, Ames.

Guo, S., and Z. Feng. 1984. Studies on resistance of soybean varieties to soybean pod borers. *In* S. Wong, D. Boethel, R. Nelson, and W. Wolf, [eds.,], Proc. 2nd U.S.-China Soybean Symp., OICD-USDA, Changchun, China.

Hammond, R. B. 1994. Japanese beetle, pp. 64–65. *In* Handbook of Soybean Insect Pests, L. G. Higley and D. J. Boethel, [eds.], Entomological Society of America, Lanham, MD.

Hammond, R. B. and R. L. Cooper. 1999. Antibiosis of released soybean germplasm to Mexican bean beetle (Coleoptera: Coccinellidae). J. Entomol. Sci. 34: 183–190.

Hammond, R. B., L. W. Bledsoe, and M. N. Anwar. 1995. Maturity and environmental effects on soybeans resistant to Mexican bean beetle (Coleoptera: Coccinellidae). J. Econ. Entomol. 88: 175–181.

Hartman, G., H. Hobbs, L. Domier, W. Pedersen, D. Eastburn, E. Levine, J. Spencer, and S. Isard. 2001. Soybean viruses in Illinois, pp. 64–69. *In* Illinois Crop Protection Technology Conference, University of Illinois at Urbana-Champaign.

Layton, M. B., D. J. Boethel, and C. M. Smith. 1987. Resistance to adult bean leaf beetle and banded cucumber beetle (Coleoptera: Chrysomelidae) in soybean. J. Econ. Entomol. 80: 151–155.

Levine, E., and H. Oloumi-Sadeghi. 1996. Western corn rootworm (Coleoptera: Chrysomelidae) larval injury to corn grown for seed production following soybeans grown for seed production. J. Econ. Entomol. 89: 1010–1016.

Nault, B. A., J. N. All, and H. R. Boerma. 1992a. Influence of soybean planting dates and leaf age on resistance to corn earworm (Lepidoptera: Noctuidae). Environ. Entomol. 21: 264–268.

Nault, B. A., J. N. All, and H. R. Boerma. 1992b. Resistance in vegetative and reproductive stages of a soybean breeding line to three defoliating (Lepidoptera: Noctuidae) pests. J. Econ. Entomol. 85: 1507–1515.

Onstad, D. W., M. G. Joselyn, S. A. Isard, E. Levine, J. L. Spencer, L. W. Bledsoe, C. R. Edwards, C. D. DiFonzo, and H. Willson. 1999. Modeling the spread of western corn rootworm (Coleoptera: Chrysomelidae) populations adapting to soybean-corn rotation. Environ. Entomol. 28: 188–194.

Pedigo, L. P. 1994. Bean leaf beetle, pp. 42–44. *In* L. G. Higley and D. J. Boethel, [eds.], Handbook of Soybean Insect Pests. Entomol. Soc. Amer., Lanham, MD.

Rufener II, G. K., R. B. Hammond, R. L. Cooper and S. K. St. Martin. 1987. A larval antibiosis screening technique for Mexican bean beetle resistance in soybean. Crop Sci. 27: 598–600.

SAS Institute. 1988. SAS/STAT User's Guide, Release 6.03 Edition. SAS Institute, Cary, NC.

Spencer, J. L., S. A. Isard, and E. Levine. 1999. Free flight of western corn rootworm (Coleoptera: Chrysomelidae) to corn and soybean plants in a walk-in wind tunnel. J. Econ. Entomol. 92: 146–155.

Spencer, J., S. Ratcliffe, S. Isard, E. Levine, C. Pierce, and S. Rondon. 2001. Western corn rootworms in the 21st century: new research on an old problem, pp. 113–114. *In* Illinois Crop Protection Technology Conference, University of Illinois at Urbana-Champaign.

Sullivan, M. J., and D. J. Boethel. 1994. Soybean looper, pp. 68–70. *In* Handbook of Soybean Insect Pests, L. G. Higley and D. J. Boethel, [eds.], Entomological Society of America, Lanham, MD.

Talekar, N. S., and B. S. Chen. 1994. Characterization of resistance to limabean pod borer (Lepidoptera: Pyralidae) in soybean. J. Econ. Entomol. 87: 821–825.

Van Duyn, J. W., S. G. Turnipseed and J. D. Maxwell. 1971. Resistance in soybeans to the Mexican bean beetle. I. Sources of resistance. Crop Sci. 11: 572–573.

Van Duyn, J. W., S. G. Turnipseed and J. D. Maxwell. 1972. Resistance in soybeans to the Mexican bean beetle. II. Reactions of the beetle to resistant plants. Crop Sci. 12: 561–562.